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Mineralogical composition of sediment determines the preference for smooth particles by caddisfly larvae during case construction

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Abstract. 1. The mineralogical/petrological composition of the substratum influences aquatic organisms in several ways. However, the actual mechanisms are often unclear. Some caddisfly larvae actively concentrate smooth quartz particles in their portable cases thus producing a smooth inner surface of the case wall.

2. The particle surface-roughness preference of *Perissoneura paradoxa* (Odontoceridae) McLachlan inhabiting granite areas in relation to the mineral composition and surface roughness of sediment particles was examined.

3. Field surveys revealed that quartz was consistently smoother than other minerals but that it became rougher in larger size fractions, and the relative abundance of quartz decreased in larger size fractions. Consequently, smooth particles were less abundant in larger size fractions of the sediment. When larval cases were compared with sediment, quartz was actively concentrated in smaller cases of early instar larvae but was gradually less abundant in larger cases of well-grown larvae. Because larvae use larger particles as they grow, late instar larvae develop an unselective choice of mineral types.

4. Subsequently, we experimentally forced the larvae to choose from a mixture of equal amounts of two artificial particles that had different textures (rough and smooth). The proportion of smooth particles chosen by larvae gradually decreased as they grew larger.

5. These results indicate that the larvae varied in their degree of preference according to particle availability in the surrounding sediment, which is governed by mineral composition and weatherability. We suggest that case-bearing caddisfly can adapt to the local sediment environments by varying their standard and/or criteria for material choice. In this study, the possible mechanism for the variation is discussed.

Key words. Confocal laser scanning microscope (CLSM), construction behaviour, material choice, phenotypic plasticity, sediment geology, surface roughness, Trichoptera.

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Introduction

In aquatic systems, inorganic substrata are often the main habitat of benthic animals. Many previous studies have investigated sediment–animal relationships [reviewed by Snelgrove and Butman (1994)]. In recent years, the mineralogical/petrological composition of sediment has been found to affect community structure, settlement and/or growth of aquatic organisms (e.g. Cerrano *et al*., 1999; Boyero, 2003; Maradonna *et al*., 2003). However, little is known about the actual mechanisms involved, particularly for macroorganisms.

Many benthic animals construct burrows, cases, and retreats composed of sediment (e.g. lugworms, bivalves, crustaceans, chironomids, mayfly or caddisfly larvae, and amoebae). Many of these are often selective in their choice of building material, using various criteria such as size, shape, gravity or the surface texture of the sediment particles [reviewed by Dudgeon (1990)]. Consequently, they often actively concentrate particular mineral and/or rock types in their constructions (e.g., Fager, 1964; Gaino *et al*., 2002; Dafoe *et al*., 2008). These biological activities and accompanying mineral aggregation/segregation are important factors not only for the builder itself but also for the environment and the diagenesis of the surrounding sediment (Dafoe *et al*., 2008; Zorn *et al*., 2010). However, little is known about the functional significance of this mineral selectivity. Okano *et al*. (2010, 2011) reported that the larvae of caddisfly species in the family Odontoceridae (Trichoptera) actively concentrate quartz into their portable cases, possibly because they prefer smooth particles (microscale roughness). Most case bearers typically line the inner surface of the case wall with silk to create a smooth surface (Williams & Pennak, 1980), thereby decreasing the internal friction between the larval body and the case wall (Okano & Kikuchi, 2009). In the Odontoceridae, however, larvae use silk only to bind the particles together and not to line the internal wall of the case (Wiggins, 2004).

Given this preference of odontocerid larvae for smooth particles, we were interested in their choice of building materials in relation to the availability of the preferred smooth particles, such as quartz. When smooth particles are scarce, the cost of searching for them would be high, which could lead to the acceptance of suboptimal materials (Hansell, 2005). Therefore, we hypothesised that the strength of preference for smooth particles would vary based on the availability of materials in the surrounding sediment. It is well known that caddis larvae flexibly use case-building materials that are similar to the preferred one when the preferred material is unavailable (Copeland & Crowell, 1937; Hanna, 1961; Statzner *et al*., 2005). However, standard and/or criteria for the material choice are typically assumed to be species-specific and unaffected by resource availability (but see Otto & Svensson, 1980).

In a certain area with granite geology, the abundance of smooth particles would progressively decrease in the larger size fraction because (i) the proportion of quartz particles decreases in larger sediment fractions and (ii) the surface of feldspar, which is more abundant in this size fraction, is generally rougher than that of quartz (Anbeek *et al*., 1994). In such a sedimentary environment, we observed that cases of smaller Odontoceridae larvae (early instar) contained a high frequency of quartz particles (Fig. 1a), whereas larger grown larvae predominantly used feldspar (Fig. 1b). We can hypothesise the reasons for this difference are: (i) the differences in mineralogical composition of the sediment among the size fractions and (ii) the larvae use larger case particles as they grow. Therefore, based on our hypothesis, we can predict the larval preference (standard for choice) for smooth particles would decrease as the larvae grew.

In this study, we focussed on a larva of the Odontoceridae species, *Perissoneura paradoxa* McLachlan, from a small stream on Mt. Maya where the underlying geology is granite. Our objective was to evaluate variations in preferences for smooth particles with larval size (i.e. larval growth) in relation to the size-dependent mineralogical composition of sediment particles. First, we compared the texture (surface roughness) and mineral composition of particles used in the natural case with those of particles in the surrounding sediment. In a subsequent laboratory experiment, we forced the larvae to choose from a mixture of equal parts of two types of artificial particles (smooth and rough). This allowed us to evaluate variations in larval preferences.

Methods

Study area and species

All samples of *Pe. paradoxa* larvae, their cases, and sediment grains were collected from a small stream on Mt. Maya (Zizou-Dani, 34°43′N, 135°11′E, which corresponds to 'Site 4' in Okano *et al*., 2011) in September 2007 when the larvae were abundant. The stream is oligotrophic and situated within a broadleaf forest (first to second order; <2-m wide and <25-cm deep). The area consists exclusively of granite (Kasama, 1968) and the sandy sediment is thus dominated by quartz, K-feldspar, plagioclase feldspar (hereafter abbreviated plagioclase), and their complexes. The larvae construct cylindrical portable cases with these mineral particles and do not line the inner case wall with secreted silk (Wiggins, 2004). Their microhabitat was typically limited to sluggish flow areas (pools between rapids and edges of the stream). In this area, two species of Odontoceridae, *Pe. paradoxa* and *Psilotreta kisoensis* Iwata (hereafter abbreviated to *Ps.kisoensis*), share the same habitat. Although the shape of their cases is generally similar, the particle size of cases built by full-grown *Pe. paradoxa* is larger than that of *Ps. kisoensis*, relative to body and case size (Okano *et al*., 2011). The particle preferences of sympatric *Ps. kisoensis* larvae were described by Okano *et al*. (2011).

We collected larvae with their cases at various growth stages (second to fifth instar) by hand or with forceps. Particles from the top layer of the sediment (about 5 cm) were collected with a scoop randomly at three areas where the larvae were abundant and placed in 100-ml plastic bottles. The larvae were held in a cooler and transported to the laboratory immediately after collection. Then, larvae were randomly separated into two

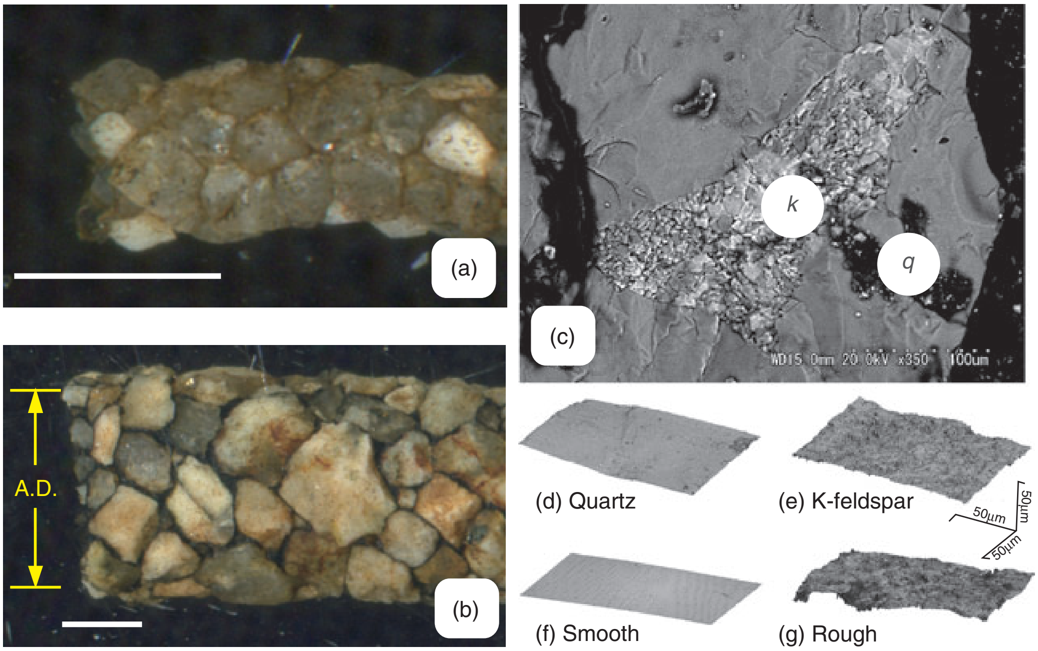

Fig. 1. Anterior end of (a) a small immature case (second instar) and (b) larger mature case (fifth instar) of *Perissoneura paradoxa* larva ('A.D.' indicates aperture diameter of the anterior end of the case). White and yellowish white particles are K-feldspar and grey particles are quartz. White bars are 2 mm in size. (c) Surface of a particle that is a mixture of quartz (q) and K-feldspar (k) taken using a scanning electron microscope (SEM). (d)–(g) picture of surface texture taken by a confocal laser scanning microscope (CLSM), (d) quartz, (e) K-feldspar, (f) smooth artificial particle, and (g) rough artificial particle.

groups; one for the measurement of case particles and one for a particle choice experiment.

Determination of particle surface roughness for experiments

To quantify the roughness of particles, we prepared sub-samples of sand particles from three sediment samples and 25 larval cases of the various instar stages (second instar: 5 individuals; third instar: four individuals; fourth instar: 13 individuals; and fifth instar: 3 individuals). The diameter of the anterior aperture of the cases (Fig. 1b) and the head width of larvae were measured under a binocular microscope using a scale attachment in the eyepiece. We employed the internal diameter as an indicator of size for the larvae and their cases (i.e. larval growth). Next, we removed eight particles from the anterior end of each case (this end contains the most recently deposited particles). Thus, we prepared 200 case particles (8 particles × 25 larvae). The scooped samples of stream sediment were washed and dried at 60 °C in the laboratory. From one of the three samples, we selected 100 sediment particles of each of six size fractions (0.25–0.50, 0.50–0.10, 1.00–1.50, 1.50–2.00, 2.00–2.50, and 2.50–3.00 mm measured along the major axis) under a binocular microscope. These particles were again washed and air-dried for measurement. In a pilot study, we compared mineral composition (100 particles per size fraction), size fraction (a granulometric analysis by sieving), and surface roughness (20 particles per size fraction) among the three size fractions (0.50–0.10, 1.00–1.50, and 1.50–2.00 mm) of the three sediment samples. We saw no major difference in these characteristics so we chose to measure for one of the three samples.

We measured the surface roughness of the particles from the larval cases and from the surrounding sediment using a confocal laser scanning microscope (CLSM, VK-8500; Keyence Corp., Osaka, Japan) owned by the Tohoku University Museum. The CLSM emits a laser beam (658 nm) and scans light reflected from the surface of the sample [1024 (x-axis) × 768 pixels (y-axis) × optional z distance with a 0.01-μm pitch] under an objective lens at 100 × magnification [lens range, 149.146 (x-axis) × 111.859 μm (y-axis)]. The vertical z distance was defined as the distance between the shortest and the longest detectable light reflections. The three dimensions of reflected light can be used to determine the surface roughness. We quantified particle roughness (Ra) as the arithmetic mean of the absolute values of the distances from the mean line of the profile as follows:

$$Ra = \sum |Rn|/n \tag{1}$$

where Rn is the distance (μm) from the mean line to the profile measured by CLSM and n is the number of measurement points. A mean line is found that is parallel to the general surface direction and divides the surface in such a way that the sum of the areas formed above the line is equal to the sum of the areas of the profile formed below the line. The surface of the particles was coated with carbon *in vacuo* to minimise reflections that could saturate the receiving detectors.

It is difficult to separate surface profile roughness from surface waviness (larger scale undulation which contributes to particle shape) when waviness is complex. To decrease the effect of waviness, we used the mean *Ra* of five squares [40 (x-axis) × 40 (y-axis) μm] that were randomly clipped from the full image (149.146 × 111.859 μm). Narrowing down and averaging the areas minimised the effects of waviness and irregular crevices or bumps.

For case particles, we measured the surface roughness of the inward-facing surface, whereas for sediment particles, we measured the surface roughness of the largest area of each particle because larvae generally bind and arrange the particles in such a way that the largest area lines the inner wall surface of the case. The roughness of sediment particles in two size fractions (0.50–0.10 and 1.00–1.50 mm) was measured previously by Okano *et al*. (2011).

The mineral types (quartz, plagioclase, K-feldspar or a mixture) of the particles were identified under a binocular microscope before carbon coating. For uncertain mineral particles, we measured the chemical components of the samples using a scanning electron microscope equipped with an energy-dispersive X-ray spectrometer (SEM-EDX: HITACHI S-3000H; Hitachi High-Technologies Corp., Tokyo, Japan and HORIBA EMAX7000; Horiba. Ltd., Kyoto, Japan) set at 20 kV with a beam current of 0.3 nA after carbon coating. For complex rocks, we regarded the particle as a 'mixture' when any of the minerals did not occupy an area of more than 70% of the measured face of the particle, whereas we regarded the particle as 'quartz' when quartz occupied more than 70% of the measured face of the particle (similarly, for plagioclase and K-feldspar). Finally, we evaluated the proportion of the number of each mineral particle as the relative composition of each mineral species.

Particle choice during case construction

To experimentally evaluate the preference of 25 larvae for smooth particles at various growth stages (third instar: 3 individuals, fourth instar: 17 individuals, fifth instar: 5 individuals), we followed the same experimental design as Okano *et al*. (2011). The diameter of the anterior aperture of cases (Fig. 1b) and the head width of larvae were measured under a binocular microscope. Next, we induced repair of the anterior portion of the case by removing one-third of its length, providing new particles for the purpose. This procedure is generally used for investigating case material selection and construction behaviour in caddisfly larvae (Hanna, 1960; Stuart & Currie, 2002).

We prepared two types of inorganic particles with different surface roughness (rough and smooth) for the larvae to use. These particles were prepared by crushing larger materials with a hammer. The rough particles were derived from ceramics ('Color Ceramic Sand White for Freshwater Aquarium'; Kamihata Corp., Hyogo, Japan) and the smooth particles were derived from glass (Alts Corp., Osaka, Japan). Both types of particle were white. The surface roughness of the two types of artificial particles was significantly different (Okano *et al*., 2011) (rough: $Ra = 1.02 \pm 0.33$ μm, mean ± SD; smooth: $Ra = 0.04 \pm 0.01$ μm; t-test, $t = -9.47$, d.f. = 9.02, $n = 10$, $P < 0.0001$; Fig. 1f,g). After crushing the source materials, we sorted the particles into four size classes (0.25–0.5, 0.5–1.0, 1.0–2.0, and 2.0–3.0 mm) using a sand strainer. Next, we mixed these four size classes in equal proportions (by mass), separately, for the two types of particles. The two types of particle were then mixed in an equal ratio (by mass). There was no difference in the number of particles to weight ratio between the two types (binominal test, $P = 0.42$). The two types of particle were of the same size range, but were non-uniform in shape. However, Okano *et al*. (2010, 2011) demonstrated that the material (ceramic, brick or glass) and shape of the particle had little effect on larval preferences compared with the effect of surface roughness.

We placed the 50 : 50 mixture of the two types of particles in plastic dishes (5 × 5 cm) submerged in a plastic aquarium (50 × 30 cm) filled with dechlorinated tap water (9–15 °C, LD 12:12 h). The larvae with damaged cases were placed in the dishes and allowed to choose particles from the mixture to repair their cases (one individual per a dish). They could not clamber over the 3.5-cm dish wall. The experimental condition was lentic but well aerated, which mimicked the natural habitat. Particle surface-roughness preference is not affected by differences in lentic/lotic environments (Okano *et al*., 2010). Fish meal ('Tetra Corydoras'; Tetra Japan Corp., Tokyo, Japan) was fed at intervals of 2 days. The experiment ended after 14 days and the larvae were preserved in vials filled with alcohol. The artificial particles used to repair the cases were then counted under a binocular microscope.

Statistical analysis

Data analysis was performed using R software (R 2.11.0). We evaluated the surface roughness of natural case particles (Y) associated with larval size (i.e. the anterior aperture diameter of the original case; X) using a non-linear regression model: $\mathrm{Y} = \alpha + \beta \ln \mathrm{X}$, where α and β are constants. The model was selected from five potential models which, apart from the non-linear regression model, also included $\mathrm{Y} = \alpha + \beta\mathrm{X}$, $\mathrm{Y} = \alpha[1 - \exp(-\beta\mathrm{X})]$, $\mathrm{Y} = \alpha - \beta \exp(-\gamma\mathrm{X})$ and generalised linear model (GLM) with a gamma distribution, using Akaike's Information Criterion (AIC). The α and β constants, used in three non-linear regressions other than GLM, were adjusted using NLS (non-linear least squares) function (details are available in http://stat.ethz.ch/R-manual/R-patched/library/stats/html/nls.html) (Crawley, 2005).

To evaluate the preference of larvae for smooth particles (i.e. the proportion of smooth artificial particles used for case repair) in relation to larval size (aperture diameter), we used a non-parametric generalised additive model (GAM) with binomial errors and a logit link. GAM is a generalised linear model with a linear predictor involving the sum of the smooth function of covariates, which allows flexible specification of the dependence of response on the covariates (Wood, 2006). The optimal number of smooth terms was estimated with an unbiased risk estimator (UBRE; Craven & Wahba, 1979).

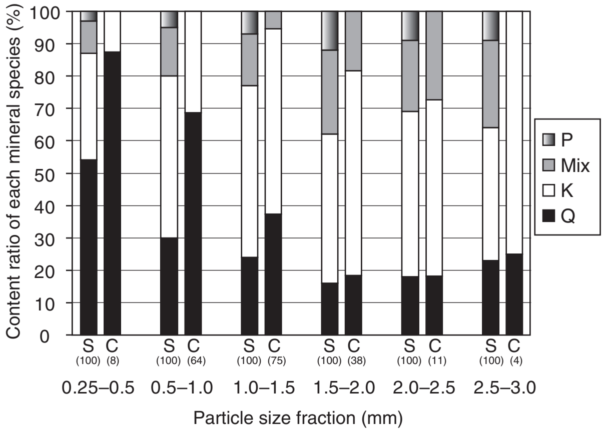

Fig. 2. The relative proportion of each mineral species (based on number of particles) according to size fraction in sediment (S) and larval case (C). (Number) = Sample size (number) of particle. Q: Quartz. K: K-feldspar. Mix: Mixture. P: Plagioclase.

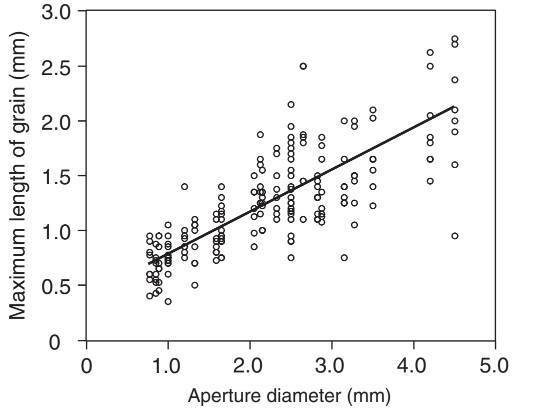

Fig. 3. The relationship between the aperture diameter of larval cases and particle size at the anterior end. The line represents the predicted values calculated with a single linear regression ($Y = 0.37X + 0.46$, $r^2 = 0.60$, $P < 0.00001$).

Finally, we used the χ^2-test to analyse the significance of the model fit.

Results

Mineralogical composition and surface roughness of particles in stream sediment and natural cases

Sediment particles. Quartz content was highest in the 0.25–0.5 mm size fraction (54%; Fig. 2) and decreased in the remaining fractions (until 16–23% in 1.5–3.0 mm). Using the CLSM we could clearly determine that the surface of quartz particles was smoother relative to feldspar (Fig. 1c–e). Indeed, quartz particles were smoother than all other minerals over all size fractions (Table 1), yet they became progressively rougher in the larger size fraction (Ra = 0.55–0.75 μm in the 0.25–1.0 mm fraction to >1.1 μm in the 2.0–3.0 mm fraction; Table 1). K-feldspar was the second smoothest mineral species (Ra = 0.832–1.14 μm) and was relatively abundant throughout all size fractions (33–53%). Compared with quartz, K-feldspar showed no specific trend in proportion or roughness over the size fractions. Plagioclase was consistently roughest (Ra = 1.17–2.22 μm) and was a minor component (less than 10%) relative to quartz and K-feldspar. Overall, the smooth particle content gradually decreased in the larger size fractions ('Whole' in Table 1) as a result of a decrease in quartz content and an increase in quartz roughness.

Larval case particles. The anterior aperture diameter of the larval cases was positively correlated with the particle size of the anterior end of the case ($P < 0.00001$; Fig. 3), suggesting that the larvae use larger particles as they grow. In addition, there was a significant positive correlation between aperture diameter and surface roughness of the anterior end of the case ($P < 0.00001$; Fig. 4), illustrating that the larvae also use rougher particles as they grow. In terms of mineralogical composition, quartz was abundant in smaller cases, whereas the K-feldspar content increased in larger cases [Fig. 4; quartz rate: 84.4% (in an average) in case aperture <1-mm, 61.6% in 1-mm ≤ case aperture <2-mm, 22.2% in 2-mm ≤ case

Table 1. Surface roughness (Ra, μm; mean ± SD) of each mineral species according to size fraction in larval case and sediment.

	Roughness (Ra, μm)						
	Sediment				Case		
		Mineral classification				Mineral classification	
Size fraction (mm)	Whole	Quartz	K	Plagio	Whole	Quartz	K
0.25–0.5	1.05 ± 0.511	0.686 ± 0.243	1.04 ± 0.312	1.17 ± 0.205	0.620 ± 0.210	0.569 ± 0.166	0.975*
0.5–1.0	1.29 ± 0.575	0.561 ± 0.211	1.04 ± 0.332	2.20 ± 0.384	0.553 ± 0.277	0.466 ± 0.202	0.743 ± 0.326
1.0–1.5	1.46 ± 0.619	0.729 ± 0.177	0.832 ± 0.222	2.03 ± 0.794	0.802 ± 0.352	0.620 ± 0.208	0.917 ± 0.391
1.5–2.0	1.66 ± 0.968	0.757 ± 0.265	1.25 ± 0.631	2.02 ± 0.555	0.872 ± 0.304	0.737 ± 0.473	0.922 ± 0.276
2.0–2.5	1.59 ± 0.618	1.14 ± 0.596	1.55 ± 0.567	2.09 ± 0.639	0.902 ± 0.197	0.817 ± 0.409	0.921 ± 0.0879
2.5–3.0	1.42 ± 0.690	1.11 ± 0.590	1.31 ± 0.595	2.22 ± 1.03	0.921 ± 0.434	0.820*	0.954 ± 0.525

*sample number = 1.
K, K-feldspar; Plagio, Plagioclase.

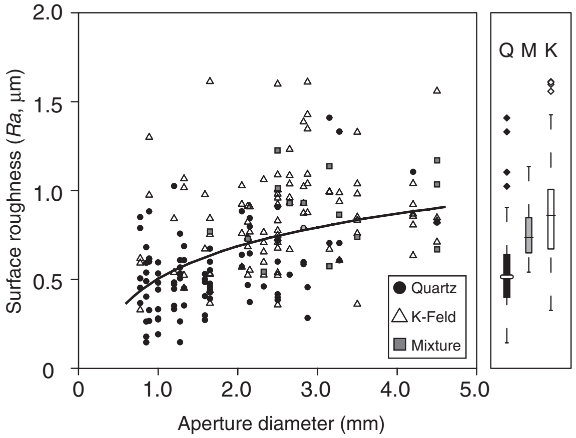

Fig. 4. The relationship between the aperture diameter of larval cases and surface roughness of case particles according to mineral species (line predicted with nonlinear regression; $Y = 0.52 + 0.30 \ln X$, $P < 0.00001$). Black circle: Quartz. Triangle: K-feldspar. Grey square: Mixture. Total values for each mineral are represented by box plots, which provide median, maximum and minimum value and 25th and 75th percentiles. Rhombuses show outliers. Black box (Q): Quartz. Grey box (M): Mixture. White Box (K): K-Feldspar.

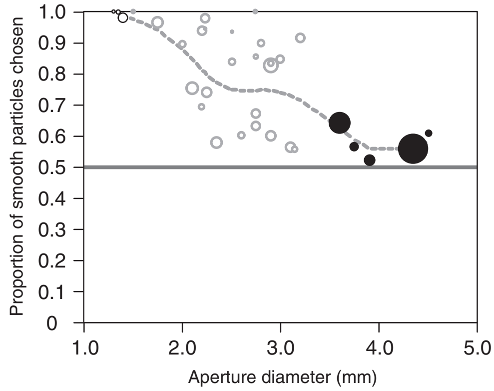

Fig. 5. Relationships between the aperture diameter of larval cases and the choice of smooth artificial particles used in larval cases in the laboratory experiments (line predicted with nonparametric generalized additive model; $r^2 = 0.89$, $P < 0.00001$). The relative size of the circle represents the total number of particles chosen by each individual (range 16–159). Open black: third instar. Open grey: fourth instar. Black: fifth instar.

aperture <3-mm, 18.8% in 4-mm ≤ case aperture]. Plagioclase was not included in the case material.

To compare specifically the roughness and mineral composition among different size fractions, we pooled the roughness data of all case particles and resorted according to the size of each case particle (Fig. 2, Table 1). Although particles used in the larval cases were consistently smoother than sediment particles, even the case particles became rougher in the larger size fractions (Table 1) because of a decrease in quartz content (Fig. 2) and an increase in quartz roughness (Table 1). Thus, the general trend in terms of roughness and mineral composition among size fractions was similar to that seen in sediment. However, we noted that the quartz content in the larval cases was higher than that in sediment throughout all size fractions, although the quartz enrichment gradually declined (Fig. 2).

Laboratory choice experiments

The proportion of smooth artificial particles chosen clearly decreased with increasing aperture diameter (GAM, $P < 0.00001$; Fig. 5), even although smooth and rough particles are equally available. Also considering Fig. 4, the degree of preference for smooth particles decreased with larval growth as the surface of the natural case particles became rougher.

Discussion

Some previous studies have suggested that quartz could have a negative effect on benthic animals (Cerrano *et al*., 1999; Bavestrello *et al*., 2000; Maradonna *et al*., 2003). The reason for such an effect is essentially unclear, although it is inferred that the effect is as a result of the toxic properties of quartz, namely its generation of silicon-based radicals (Maradonna *et al*., 2003). In contrast, our field surveys revealed that quartz is actively concentrated in larval cases as a result of larval preference for smooth surface particles as a case material. Caddisfly larvae bearing cylindrical cases prefer a smooth inner case wall, which can be interpreted as an adaptation connected to the abdominal undulation that drives the water current through the case; this could maintain adequate respiration by preventing gill abrasion and/or by smoothing undulation behaviour (Williams & Pennak, 1980; Okano & Kikuchi, 2009).

Although larvae consistently used smoother particles from the sediment to build their cases, larger case particles had rougher surfaces. This was because of a size-related decrease in content and an increase in the roughness of the quartz, which reflects sediment characteristics. Such variations in sediment characteristics can be explained by the differential weathering of granitic minerals. In this study, the roughness of the mineral surface was in the following order: quartz < K-feldspar < plagioclase. This sequence is similar to the relative rate of weathering of these minerals (Goldich, 1938). The surface of granitic mineral species becomes rougher as they are more severely weathered by chemical processes (chemical weathering; Anbeek *et al*., 1994). In addition, the weathering processes can possibly affect the relative amount of each mineral species in each size fraction. Easily weathered minerals are eliminated from the sediment by dissolution in the smaller size fraction, and the quartz content is generally higher in this fraction (approx. 0.02 mm; Ollier, 1969). This suggests that the gradual increase in the quartz content of the smaller size fractions is as a result of their hardness and resistance to chemical weathering, suggesting that plagioclase is consistently scarce because of its low resistance to weathering. However, even quartz becomes rougher in the larger size fraction, probably because of physical rather than chemical weathering. Quartz crystallises with allotriomorphic forms in rock such as granite, resulting in a rough surface at the boundary with other minerals (Miyashiro & Kushiro, 1975; Cornelius *et al*., 1985). In this study, larger quartz particles ($>$1.5 mm) typically had a bare allotriomorphic face, whereas smaller quartz particles had a smoother, freshly fractured face, possibly derived from larger particles. Therefore, smaller larvae would be more likely to actively concentrate smaller smooth quartz particles in their cases, whereas larger quartz particles would not be worth concentrating for larger larvae because of the relatively rough surfaces. This is consistent with our present results.

Subsequently, we forced the larvae to choose from a mixture of equal amounts of rough and smooth particles that had different textures. The laboratory experiments revealed that the preference for smooth particles declined with increasing larval size. Combined with the results from the field study, this indicates that caddis larvae vary their choice based on the availability of smooth particles in the surrounding sediment in the field. Other *Pe. paradoxa* populations inhabiting an area where smooth particles are constantly abundant, exhibited a strong preference for such particles even when they were fully grown (Okano *et al*., 2011). Thus, using smooth particles is potentially beneficial even for fully grown larvae, and so the fundamental factor regulating the particle preference is smooth particle abundance but not the growth stage itself (Fig. 5 is actually a spurious correlation). In this study, we showed that larvae use larger case particles as they grow and that smooth particles become progressively less abundant in the larger size fraction. Thus, the cost of searching for smooth particles increases as the larvae grow, while larvae may suffer damage to their gills or be unable to undulate effectively if the case is too rough. To achieve the best balance between cost (searching for particles) and benefit (respiration advantage) in such a sediment environment, a decrease in preference for smooth particles is likely to be more beneficial.

In our study area, two Odontoceridae, *Pe. paradoxa* and *Ps. kisoensis*, share the same habitat. However, *Ps. kisoensis* did not show variation in smooth particle preference according to larval size (see figure 6d in Okano *et al*., 2011). This is because the particle size was much smaller in the *Ps. kisoensis* larval cases (less than 1.3 mm) than in *Pe. paradoxa* cases relative to their difference in body size. Therefore, *Ps. kisoensis* larvae would not experience significant variation in sediment quality (i.e. availability of smooth particles) compared with *Pe. paradoxa*.

Nevertheless, *Pe. paradoxa* larvae should be able to construct their cases of smooth particles and save on searching cost using small particles because smooth particles are abundant in the smaller size fraction. In addition, small particles were more abundant than larger ones in the sediment. However, Okano *et al*. (2011) demonstrated that in a sedimentary environment where the relative abundance of smooth particles was similar among the size fractions, larvae exhibited no major variation in smooth particle preference according to larval size, irrespective of relative particle abundance by size fraction (i.e. small particles were more abundant than larger ones in the sediment across all locations). This indicates that larval preference is determined by the abundance of smooth particles within the appropriate size range rather than across the whole size range. Larvae may regard only particles of an appropriate size as case material (at least when particles of an appropriate size are available). There seem to be two possible reasons why the larvae do not use smaller particles. First, the amount of silk required to bind particles together increases with decreasing particle size (Smart, 1976; Becker, 2001). Second, larval cases constructed of smaller particles than that appropriate to the case size may be structurally unstable (Statzner *et al*., 2005). Larvae need rigid cases because the important function of the case is protection from predators and/or physical damage (Ross, 1956; Otto & Svensson, 1980; Wiggins, 2004). Therefore, the benefit derived from a smooth case wall constructed of even smaller particles than those preferred may not exceed the sum of these various costs (e.g. the extra cost associated with the secretion of silk and reduced case stability).

Construction of biological structures is a fundamental behaviour for many animals. However, their construction behaviours are typically assumed to have no meaningful variation within species and to be unaffected by the physical environment. In contrast, our previous study (Okano *et al*., 2011) showed that the two Odontoceridae, *Pe. paradoxa* and *Ps. kisoensis*, had a distinct variation in particle surface roughness preferences among geographically distant populations. Local populations develop different particle preferences based on local geology. However, the relationship between variations in larval preference and particle availability within a single population was not clear. Conversely, we demonstrated that *Pe. paradoxa* varied its preference, even over its lifetime, based on the variation in the abundance of smooth particles in the sediment. Some caddisfly species are known to ontogenetically switch between using organic and inorganic particles for their case material. Although Otto and Svensson (1980) proposed an idea that ontogenetic switches in particle selection between organic and mineral particles during larval life were related to the relative abundance of these materials, there is no solid evidence to support this idea.

Another question arose as to how variations among distant populations (e.g. geographical variation) and during larval life have occurred. These heterogeneities within species may be caused by innate genetic variation and/or acquired variation (Okano *et al*., 2011). In addition, these two types of variations (among populations and during larval life) resemble each other, but their actual mechanisms may be different. Okano *et al*. (2011) showed that the odontocerid population had greater variation in individual preference for smooth particles when smooth particles were less abundant (Figure 5 in Okano *et al*., 2011). In other words, even when smooth particles are rare, some individuals still prefer them to such a degree that they incur considerable cost to obtain them. In contrast, our present study showed no individual preferred smooth particles when these were rare (i.e. when larvae grew larger). We have no definite answer for this contradiction. However, the larval population that was the focus in this study differed somewhat in that the abundance of smooth particles varied, whereas populations in the previous study (Okano *et al*., 2011) experienced a relatively constant availability of smooth particles through their lifespan (e.g. the relative abundance of smooth particles was similar among the size fractions). When the environment varies within the lifetime, phenotypic plasticity can be favoured as it enables a phenotype to better adjust to its environment (Dukas, 1998). Thus, one possibility is that the geographical variation detected in our previous study was mainly based on innate genetic variation, whereas the variation during larval life detected in the present study was because of phenotypic plasticity but not ontogenetic development. Large individual variation in an environment with a constantly low abundance of smooth particles indicates that a cost-increasing strategy to exploit smooth particles (i.e. a relatively strong preference) is equally as adaptive as a cost-saving strategy (i.e. a relatively low preference). In this case, plasticity would not be favoured as it brings no extra benefit but involves some costs (e.g. maintenance costs). However, when the smooth particle availability is variable, this broad cost-benefit equilibrium may be lost, and thus greater plasticity can be evolved. If this were so, the larvae would all have a similarly reduced preference (Fig. 5) because they would be able to determine the particle availability in the sediment. Larvae of *Pe. paradoxa* and *Ps. kisoensis* often cannibalise conspecifics (probably size-structured cannibalism, J. Okano, pers. obs.), although the frequency in natural habitats is unclear. Thus, larvae may need to grow faster than conspecifics by achieving the best balance between cost and benefit. In addition, they are geographically isolated with a limited gene flow within 10 km (Eguchi & Matsumoto, 1983; Matsumoto & Eguchi, 1990). Therefore, intra-specific competition within a certain limited area may promote evolution of particle choice behaviour particular to a local sediment environment. Gallepp (1974) also claimed that cannibalism was a possible agent of selection pressure in connection with case construction by *Brachycentrus occidentalis* Banks. To test these implications, future studies should investigate the mechanisms controlling case-building behaviour.

Many caddisfly species have portable cases of various shapes and forms that are constructed using various materials. In addition, some caddisfly species are known to change case material ontogenetically (Otto & Svensson, 1980) or as a result of chemical cues (Boyero *et al*., 2011). Therefore, the choice of material and the shape of caddisfly larval cases are remarkably diverse. However, the actual mechanisms associated with the adaptive radiation of case construction behaviour are unclear. Thus, the intra-specific heterogeneity in particle preferences, revealed here, may be an important key to understanding the great divergence of caddisfly cases.

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